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ON THE OCCURRENCE OF PAIRED MADREPORIC PORES AND PORE-CANALS IN THE ADVANCED BIPENNARIA LARVÆ OF ASTERINA (PATIRIA) MINIATA TOGETHER WITH A DISCUSSION OF THE SIGNIFICANCE OF SIMILAR STRUCTURES IN OTHER ECHINODERM LARVÆ.

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INTRODUCTION.

Ever since the theory became current that the bilaterally symmetrical larvæ of echinoderms afford phylogenetic evidence that this group of radially symmetrical animals was derived from bilaterally symmetrical ancestors, larvæ that showed more than the normal tendencies toward persistent bilaterality have had a special significance.

Normally, the first evidence of the encroachment of the adult radial symmetry upon the the larval bilaterality is seen in the development of a distinct hydrocœl with a madreporic pore and pore-canal on the left side, and none on the right. This failure of the right side to keep pace with the left has been considered as the mechanical cause for the twisting around of the serially repeated primordia of the radial water canals and the assumption of the adult radial symmetry.

The occurrence, therefore, in the larvæ of at least two classes of echinoderms, of paired right and left madreporic pores, pore-canals, and other derivatives of the hydrocœls, looks like the persistence of the ancestral bilateriality and tends to strengthen the current theory as to echinoderm phylogeny.

As early as 1892 Field, in his account of the larval development of *Asterias vulgaris,* described the transitory appearance in all

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larvæ aged about three and a half days of a strictly bilaterally symmetrical condition of the hydrocœls, madreporic pores, and pore-canals. Soon after this period the right madreporic pore closes and the pore-canal, without an external opening, persists for a short time and then entirely disappears.

Several continental writers had observed the occasional occurrence in asteroid larvæ of paired madreporic pores, but had considered the condition as a pathological one. Field, however, maintains that there normally occurs, in *Asterias vulgaris* at least, a transitory stage in which bilateral madreporic pores exist, and considers this condition as "a true ontogenetic character, and of very considerable phylogentic significance." Gemmill (1912) was able partially to confirm Field's observations of the occurrence of paired water pores in the genus *Asterias,* finding this condition in fifty per cent. of larvæ of *Asterias glacialis* and in about ten per cent. of those *Asterias rubens.* He also states that in all cases the water-pore soon closes.

Paired echinus-organs, madreporic vesicles, and other derivatives of the right hydrocœl, were observed by MacBride (1911) in two very advanced Plutei, one of *Echinus miliaris* and the other of *Echinus esculentis.* A similar condition was observed by Grave (1911) in a single Pluteus of the sand-dollar *Mellita pentapora,* though the figure shows the two madreporic canals making exit through a single median dorsal madreporic pore.

Paired Madreporic Pores in Asterina Larvæ.

During the months of April, May and June, 1920, I had occasion to observe the development of a very large number of cultures of larvæ of *Asterina* (*Patiria*) *miniata* at Pacific Grove, California. In one culture consisting of otherwise normal, healthy larvæ three weeks old, I noticed a larva with two perfect madreporic pores and pore-canals. Further search, involving a complete census of all the larvæ in the culture, revealed twenty-six more larvæ with right madreporic canals in some cases as well developed as the left; but in others with the right pore closed and the pore-canal smaller than the one on the left. More than half of all the advanced larvæ in this culture had the double madre-

poric pores or at least double pore-canals, while the remainder of the larvæ were quite typical. After a prolonged search in other cultures of *Asterina,* I was unable to discover any other larvæ with double madreporic pores.

These double-pored larvæ were carefully watched and attempts were made to rear them by introducing diatoms collected from

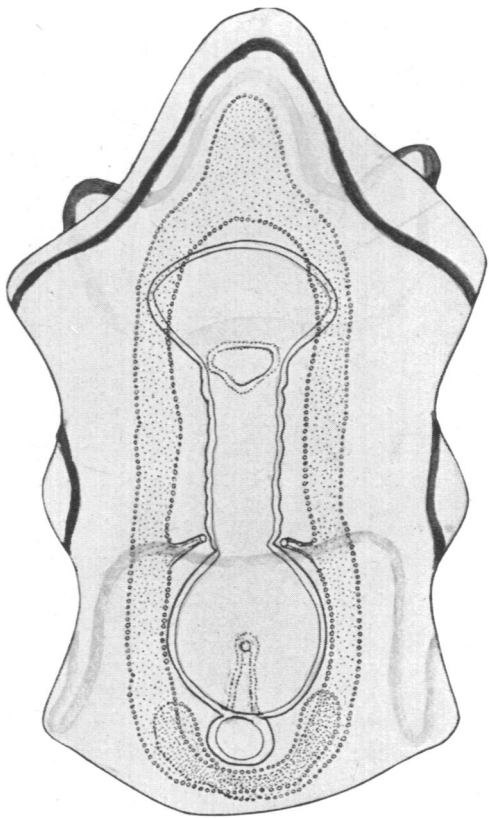

FIG. 1. Dorsal view of largest bipennaria, viewed as a transparent object. The hydroenterocoel cavities are shown stippled. Note both left and right madreporic pores, opening far apart; distinct pore-canals on both sides.

the kelp found in the tide pools inhabited by *Asterina.* They fed to some extent on several species of diatoms, but made no progress beyond the condition in which they were when the double-pored character was first noticed. Instead, they slowly retrogressed in

differentiation, became sluggish, and died without having begun to metamorphose. Throughout their lives they remained bilaterally symmetrical and observations made at the end of the fourth week, shortly before the culture began to die out, showed that the right madreporic pore was still open in several of the largest bipennariæ. While the larvæ were still active and in good health, several specimens were quieted with chloretone and mounted for

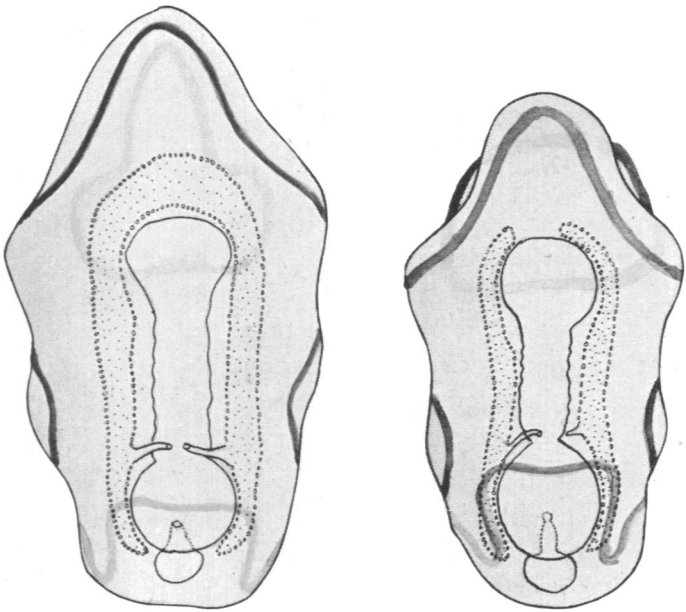

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FIG. 2. Dorsal view of a somewhat less advanced bipennaria with madreporic pores close together but both open.

FIG. 3. Dorsal view of one of the least advanced bipennariæ with right madreporic pore closed, but with distinct pore canal on the right side.

microscopic study. These were drawn with camera lucida and three of these drawings are shown in Figs. 1–3. The largest larva in the culture is shown in Fig. 1. Its length was a little over 7 mm. The anterior hydroenterocœl pouches have become completely fused in front of the oral funnel and have grown forward into a median pre-oral cœlomic cavity. The right and left body cavities are equally well developed throughout and each has grown posteriorly beyond its own side and has curled round

the intestine, so as to have its blind end pointed forward on the opposite side of the body. Thus these two posterior outgrowths cross one another and encroach on each other's territory, a condition that could not well represent any ancestral state, but one to be expected in a double monster such as I believe this to be. Each madreporic canal connects broadly with the dorsal wall of its respective hydrocœl, slopes slightly toward the median line, and opens by a distinct pore to the exterior. The two pores are not very close together in this specimen. The other two larvæ are a little smaller and less advanced than that shown in Fig. 1. That shown in Fig. 2 is about 6 mm. in length, has no pronounced forward growth of the preoral cœlom and does not show an overlapping of the posterior extensions of the right and left cœloms. The pores of the two pore-canals are very close together and might form one double madreporite. The specimen shown in Fig. 3 was of about the same stage of advancement as that in Fig. 2 but differs primarily in the fact that the right madreporic pore is closed and its canal is smaller and shorter than its left partner. Also the anterior cœloms have not fused.

In discussing these anomalous larvæ with Dr. Walter K. Fisher, director of the Hopkins Marine Station, I was interested to learn from him that he had, while collecting, noted adult specimens of *Asterina,* and of other species of asteroids, in which there were two madreporic plates and, correspondingly, two stone canals. This information immediately suggested to me the strong probability that these adults with paired madreporic plates must have arisen from larvæ with double madreporic pores such as I had under observation. The question would then arise as to whether this double condition in the adults would bear the same phylogenetic interpretation as has been offered for the double condition in the larvæ. If not; why not? But this involves us in a discussion of the significance of these anomalous paired structures in echinoderms.

Discussion.

Three distinct interpretations have been offered for the appearance of these anomalous right-hand elements that normally appear only on the left.

1. The first interpretation is well phrased by MacBride[1] as follows:

"The appearance of a right and left madreporic pore is the first indication of what is really the key to the understanding of Echinoderm development, viz., the fact that the two sides of the larvæ originally gave rise to precisely similar organs, but that some of these organs grew and developed on the left side while they atrophied on the right, and that thus an asymmetry was produced."

This seems to be the natural interpretation of the facts, but there are certain other facts that this interpretation does not cover. In a larva of the sand-dollar *Mellita pentapora,* Grave (1919) found that not only were the mesodermal structures, including hydrocoel, pore-canals, etc., bilaterally repeated, but also paired ectodermal pouches occurred which had no reference to the water-vascular system, but were the primordia of the nervous system. Grave is inclined to doubt the validity of interpreting this extra ectodermal pouch as a reversion to an ancestral condition, and I would fully agree with him. The occurence of adult starfishes with paired madreporic plates and stone canals also weakens the phylogentic interpretation of double pores in larvæ; for they are evidently strictly homologous structures. If the double-plate condition in the adult is to be interpreted as a reversion, of what is it an ancestral reminscence? Surely not of an ancestral starfish with radial symmetry of other organs, but bilateral madreporic structures!

2. The second interpretation of paired madreporic structures involves the idea that they are homœotic variations, in Bateson's sense. Such variations may be viewed according to Grave "as cases of perfected symmetry, the result of a long continued strain due to imperfect balance, either morphological or physiological or both, between the organism and its environment." I confess that I am unable to see the force of this interpretation. It is highly mystical in tone and savors of some internal perfecting principle or "entelechy." If such a principle were operative, the real problem would be to account for the failure of echinoderm

[1] "Text-book of Embryology," Vol. I., p. 466.

larvæ in general to continue to maintain their original bilaterality. That is a different problem altogether.

3. A third theory involves the idea that these duplicated structures are the products of twinning and this is what I believe they are. In laboratory cultures of *Asterina* (and in at least two other species of asteroids with which I have worked) there are numerous instances of twins and double monsters. The exact cause of twinning and doubling is not fully known and will not be discussed here, as I have in preparation a more extensive paper on this subject. It may be said, however, that a long series of types has been found in which the original right and left primordia of the future embryo become more or less completely physiologically isolated, and in proportion to the duration or completeness of the isolation, each half develops more or less independently of the other. The result is a series of more or less completely doubled larvæ, as follows: twin blastulæ which soon separate and develop into half-sized larvæ; gastrulæ with paired archentera; gastrulæ with paired blastopores, but with archentera fused anteriorly; early bipennariæ with the anterior end of the archenteron branched and with the beginning of a double set of hydroenterocœl pouches; and finally advanced larvæ with double madreporic pores and water canals. I have placed the type of anomalous larvæ under discussion at the end of what appears to me to be a logical series, representing the results of varying degrees of physiological isolation of bilateral halves of embryos. The type of result attained seems to depend on the time of incidence of the cause or causes of the physiological isolation in question and upon the degree of severity or duration of the causal agent, whatever it may be.

There is therefore no more justification for the use of "double-pored" larvæ of echinoderms as evidence of an ancestral condition than there is for giving a similar significance to instances of dicephaly or spina bifida in vertebrates. For they are all, in my opinion, phases of "twinning" in the broad sense and will doubtless be explicable on some general physiological basis that we shall hope to discuss in the future. Let me close with a word of caution. Beware of giving a phylogenetic interpretation to an

anomaly found in laboratory-bred larvæ of any sort. Such aberrations are more than likely to be the result of subnormal conditions and nothing more.

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